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The Falkland Islands' palaeoecological response to millennial-scale climate perturbations during the Pleistocene–Holocene transition: Implications for future vegetation stability in the southern ocean islands

ROBERT G. SCAIFE,[1] ANTONY J. LONG,[2] ALISTAIR J. MONTEATH,[1]* PAUL D. M. HUGHES,[1] MICHAEL J. BENTLEY[2] and PHILIP STONE[3,4]

[1]Geography and Environment, University of Southampton, UK
[2]Department of Geography, Durham University, UK
[3]British Geological Survey, The Lyell Centre Edinburgh, UK
[4]Falkland Islands Department of Mineral Resources, Stanley, Falkland Islands

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ABSTRACT: Oceanic island flora is vulnerable to future climate warming, which is likely to promote changes in vegetation composition, and invasion of non-native species. Sub-Antarctic islands are predicted to experience rapid warming during the next century; therefore, establishing trajectories of change in vegetation communities is essential for developing conservation strategies to preserve biological diversity. We present a Late-glacial–early Holocene (16 500–6450 cal a BP) palaeoecological record from Hooker's Point, Falkland Islands (Islas Malvinas), South Atlantic. This period spans the Pleistocene–Holocene transition, providing insight into biological responses to abrupt climate change. Pollen and plant macrofossil records appear insensitive to climatic cooling during the Late-glacial, but undergo rapid turnover in response to regional warming. The absence of trees throughout the Late-glacial–early Holocene enables the recognition of far-travelled pollen from southern South America. The first occurrence of *Nothofagus* (southern beech) may reflect changes in the strength and/or position of the Southern Westerly Wind Belt during the Late-glacial period. Peat inception and accumulation at Hooker's Point is likely to be promoted by the recalcitrant litter of wind-adapted flora. This recalcitrant litter helps to explain widespread peatland development in a comparatively dry environment, and suggests that wind-adapted peatlands can remain carbon sinks even under low precipitation regimes.

KEYWORDS: Falkland Islands; island conservation; palaeoecology; peatland; Southern Westerly Wind Belt

Introduction

Vegetation communities on small oceanic islands are particularly vulnerable to future climate change because of their often-restricted biological diversity, specialised adaptations and limited habitat availability, which impedes species ability to shift ranges (Nurse *et al.*, 2014; Harter *et al.*, 2015). Antarctic and sub-Antarctic islands in the southern oceans are expected to experience rapid temperature rises during the next century (Larsen *et al.*, 2014), and native plant taxa are likely to face increased competition from invasive species as habitats become suitable for a new range of flora (Hellmann *et al.*, 2008; Walther *et al.*, 2009; Thalmann *et al.*, 2015). Understanding the trajectory of change in vegetation communities in these islands is, therefore, essential for developing strategies for future conservation.

The Falkland Islands (Islas Malvinas) archipelago lies north of the polar front within the core of the Southern Westerly Wind Belt (49–53 °S). The islands are an unusual example of a treeless maritime environment which supports rare and endemic plant species (Upson and Lewis, 2014). During the last century, annual mean temperatures have increased by 0.5 °C in Stanley, East Falkland (Lister and Jones, 2015), and are predicted to rise a further 1.8 (±0.34) °C by 2080 (Jones *et al.*, 2013). This warming is likely to lead to decreased soil moisture (Bokhorst *et al.*, 2007) and alter plant distributions across the islands, with limited refugium availability in upland areas (Upson *et al.*, 2016). These projected temperature rises will also affect peatland ecosystems which are extensive in the Falkland Islands. In the northern hemisphere, peatland vegetation succession has been shown to occur rapidly in response to climatic changes (Barber *et al.*, 1994; Hughes *et al.*, 2006; Roland *et al.*, 2014), and is highly sensitive to changes in effective precipitation. The contemporary peatlands of the Falkland Islands exist in what are now marginal conditions for peat accumulation because of limited precipitation, and it is unclear whether these ecological systems are sensitive to changes in temperature or atmospheric moisture availability. Understanding the response of these peatlands to past and future climate variability is therefore important for the conservation of peatland vegetation (and carbon reservoirs) in the Falkland Islands.

Palaeoecology provides an important means to investigate: i) ecosystem resilience, ii) rates of environmental change, and iii) threshold responses; and iv) to test predictions of future vegetation turnover (Mauquoy and Yeloff, 2008; Willis *et al.*, 2010; Nogué *et al.*, 2017). Here we present a Late-glacial–early Holocene (*c.*16 500–6450 cal a BP) palaeoecological record from Hooker's Point (51°42′S, 57°47′W), an exposed coastal peat cliff in East Falkland. This period encompasses the Pleistocene–Holocene transition, a period that was punctuated by both warm and cold millennial-scale climate events, including the Antarctic Cold Reversal (ACR) (14 700–13 000 yr BP), a cooling event widely expressed in

*Correspondence: A. J. Monteath, as above.
E-mail: Ali.monteath@soton.ac.uk

the Antarctic ice cores in Patagonia, and across the southern oceans (Kilian and Lamy, 2013; Pedro *et al.*, 2016). By examining the palaeoecological response to these climate events we aim to assess the potential responses of sub-Antarctic island vegetation to future climate change.

The absence of any higher arboreal or larger shrub vegetation in the Falkland Islands means that palaeo-records here allow the recognition of long distance pollen, including elements from the *Nothofagus* (southern beech) forests of southern South America, such as *Nothofagus* and *Drimys* (Barrow, 1978). Changes in the abundance of these South American pollen components have been used to infer Holocene changes in the strength and/or position of the Southern Westerly Wind Belt (Mayr *et al.*, 2007; Strother *et al.*, 2015; Turney *et al.*, 2016; Thomas *et al.*, 2018). However, this approach has never been applied to Late-glacial deposits in the southern oceans, a period during which the Southern Westerly Wind Belt is suggested to have been particularly dynamic (Moreno *et al.*, 2009, 2012; Vanneste *et al.*, 2015).

Regional setting – the Falkland Islands

Physical setting

The Falkland Islands (51–53°S, 57–61°W) lie about 540 km east of southern South America, in the South Atlantic Ocean (Fig. 1). The archipelago includes over 780 islands, but is dominated by the two largest – West Falkland and East Falkland. Several upland areas occur in excess of 500 m above sea level (a.s.l.); however, the archipelago is characterised by undulating lowlands that are vegetated by acid grassland communities, predominantly whitegrass (*Cortaderia pilosa*) (Davies and McAdam 1989). The underlying, geological setting of the Falkland Islands comprises dominantly Palaeozoic quartzites and sandstones (Aldiss and Edwards, 1999; Stone, 2016). Quaternary glaciation was limited, with small glaciers confined to the highest uplands. However, periglacial deposits and landforms are common across the islands (Wilson *et al.*, 2008).

The present maritime climate of the Falkland Islands is strongly influenced by the cool sea surface temperatures of the surrounding South Atlantic Ocean (annual temperature of *c.* 6 °C; Brandini *et al.*, 2000). Locally, these are controlled by the Falkland (Malvinas) Current, an extension of the northern part of the Antarctic Circumpolar Current. The islands' climate is cool and relatively dry with a narrow range of mean monthly (February 9.5 °C, July 3.8 °C) and mean annual (6.5 °C) temperatures (1987–2000 observations: Mount Pleasant Airport). Precipitation is low (*c.* 500–800 mm yr^{-1}), but evenly distributed throughout the year (Otley *et al.*, 2008; Lister and Jones, 2015). There is some evidence for climatic gradients across the islands; the western coasts of each island receive less precipitation than the eastern coasts (e.g. 430 mm yr^{-1} at West Point Island versus *c.* 600 mm yr^{-1} at Stanley) (Otley *et al.*, 2008). The Falkland Islands lie beneath the central jet of the Southern Westerly Wind Belt with high annual and monthly mean wind speeds (in the range of 6–9 ms^{-1}), which dominantly (74%) come from the sector 200–340° (Clark and Wilson, 1992; Upton and Shaw 2002; Lister and Jones, 2015). These strong winds carry little moisture due to the orographic effect of the Andes, and precipitation is linked with southerly and easterly airflow (Thomas *et al.*, 2018).

Contemporary vegetation and previous work on the palaeoecology of the South Atlantic Islands

Although the vegetation of the Falkland Islands is not as impoverished as the Antarctic islands, the flora is considerably

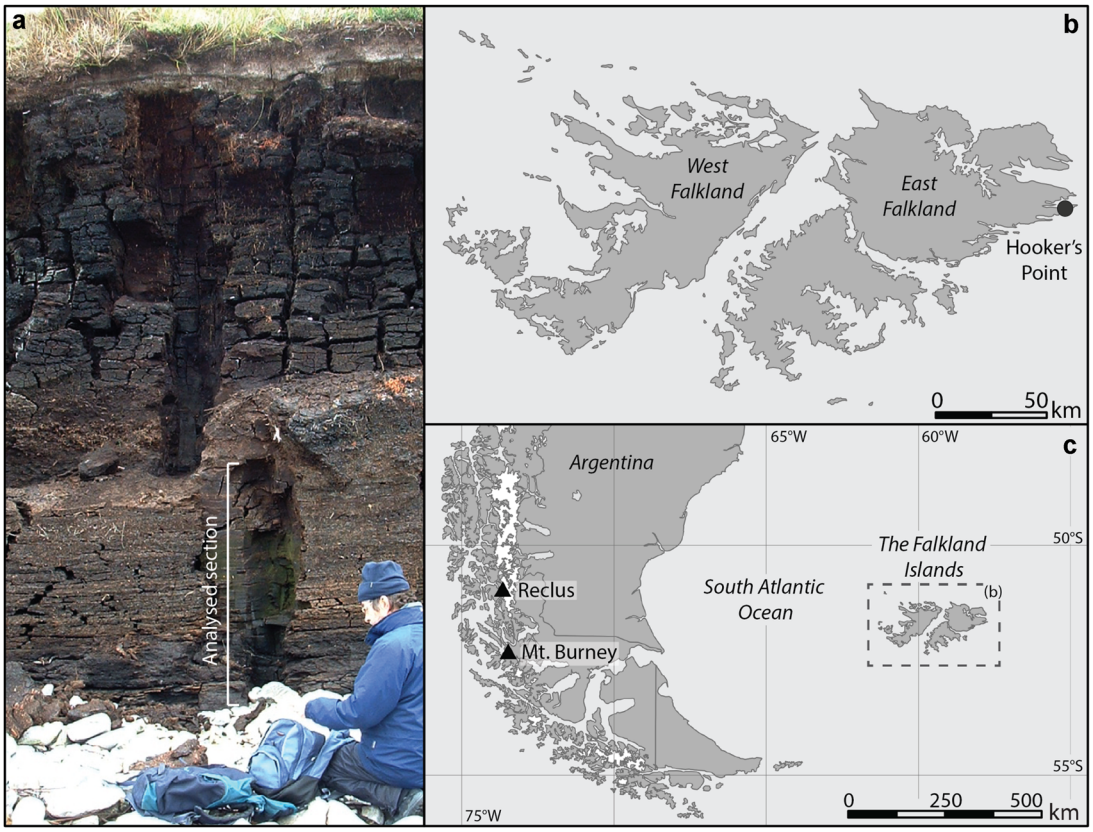

Figure 1. (a) The Hooker's Point peat section (post sampling) shown in relation to (b) the Falkland Islands, (c) southern South America and the volcanic sources (Mt. Burney ad Reclus Volcano) of cryptotephra deposits used to test the Hooker's Point age–depth model. [Color figure can be viewed at wileyonlinelibrary.com].

more restricted than Patagonia and Tierra del Fuego, with only 180 native taxa, including 14 endemic species (Upson and Lewis, 2014). Moore (1983) provides the most authoritative account of the flora and ecology of the South Atlantic islands, and this has been extensively used along with the pollen flora of Heusser (1971) and Barrow (1976) to ascertain possible pollen types and vegetation communities in this study. Other useful ecological flora are those of Moore (1968), Davies and McAdam (1989), Woods (2000) and Upson and Lewis (2014).

The present-day vegetation of coastal regions in the Falkland Islands is characterised by acid grassland, dominated by whitegrass (*Cortaderia pilosa*), and lesser occurrences of dwarf shrub heath. This latter community includes diddle-dee (*Empetrum rubrum*) with mountain berry (*Pernettya pumila),* teaberry (*Myrteola nummularia*) and Christmas bush (*Baccharis magellanica*). Ferns (*Blechnum penna-marina* and *B. magellanicum*) may be important in dry, well-drained areas, including areas of hard dry peat in the coastal zone. Tussac grass (*Poa flabellata*) was once common along the coastal fringe but is now heavily restricted through grazing pressure with an estimated loss of 80% of its range since the introduction of livestock in the 18th century (Otley *et al.*, 2008; Strange et al, 1988). Shallow peatlands occur in low-lying basins, and support communities of whitegrass. Deeper peats are characterised by cushions of *Astelia pumila* along with acidophilous plants such as sundew (*Drosera uniflora*) and, in locally waterlogged areas, *Scirpus* occurs occasionally with cushion grass (*Oreobolus obtusangulus*) and rare patches of bog moss (*Sphagnum*).

Prior to this study, there has been no continuous record of Late-glacial palaeoecology from the Falkland Islands. Barrow (1976, 1978) provides the first pollen data for the Falkland Islands (and South Georgia) and demonstrates a continuity of vegetation throughout the Holocene, and the absence of any higher arboreal or shrub vegetation. The tallest native shrubs are native box (*Hoebe elliptica*), fachine (*Chiliotrichum diffusum*) and the more recently introduced gorse (*Ulex europaea*). Further, mid–late Holocene pollen data are reported by Turney *et al.* (2016) and Thomas *et al.* (2018), while Clark *et al.* (1998) describe the palynology of thin organic horizons with ages of 36 000 to 28 000 ^{14}C yr BP. These organic lenses from Plaza Creek, East Falkland, are interbedded between mass wasting and periglacial deposits and show a grass-steppe environment. The vegetation assemblage throughout the analysed section was remarkably constant, which led Clark *et al.* (1998) to suggest that either there was little change in the environment during the period of sediment accretion or that the assemblage was insensitive to climatic change.

Hooker's Point, East Falkland section

Hooker's Point lies 3.5 km east of Stanley (Fig. 1) and was named after the eminent botanist Sir Joseph Hooker, who visited the Falkland Islands in 1842 as a member of the *Erebus* and Terror Antarctic expedition, led by James Clark Ross. The Hooker's Point peat section (51°42'S, 57°47'W) is a vertical exposure of peat lying immediately behind a small boulder beach, adjacent to Hooker's Point (Fig. 1). The peat overlies grey silt that is located close to rounded beach cobbles that comprise the upper levels of the active beach. The section extends from around 3 m a.s.l. to the present clifftop at around 8 m a.s.l. The Hooker's Point sequence is exposed by eroding wave action and must have formed part of a larger peatland system in the past. Relative sea level around the Falkland Islands reached levels close to present between *c.* 8400 yr BP and *c.* 7000 yr BP (Newton *et al.*, 2014), and therefore, Hooker's Point must have either been partially protected from erosion or have experienced significant shoreline retreat. At the time of sampling, active erosion had created a bench approximately one third of the way up the peat face (Fig. 1). The entire profile was sampled in February 2005 using a series of overlapping 50 cm and 25 cm monolith tins, which were pushed into a cleaned section face and excavated using a spade. Here, we describe the palaeoecology of the lowermost 168 cm of peat from the monolith-sampled sequence (Figs. 1,2).

Materials and methods

Chronology

Eight samples were dated using accelerator mass spectrometer radiocarbon dating (AMS ^{14}C dating): four bulk peat samples, three macrofossil samples and one wood fragment (Table 1). The plant macrofossil remains comprised at least 300 mg wet weight of the above-ground remains from higher plants. Where presence allowed, the stems of *Sphagnum* were preferred as these are representative of *in situ* peat surface. In all cases, plant macrofossils were repeatedly washed in deionised water and cleaned of all fungal hyphae and rootlet material before AMS ^{14}C dating.

A Bayesian age–depth model (Fig. 2) was developed from eight AMS ^{14}C dates using OxCal 4.2.3 (Bronk Ramsey, 2017), and the SHCal13 calibration curve (Hogg *et al.,* 2013). A *P_Sequence* depositional model was run with outlier detection (Bronk Ramsey 2008, 2009a) and a variable *k* factor (depositional events per unit length: cm^{-1}) (Bronk Ramsey and Lee, 2013). One radiocarbon date (Beta-241336) suggests a slight age reversal. This, however, did not reduce the overall model agreement to <60%, and so was retained in the final age–depth model (Bronk Ramsey, 2009b). The final age–depth model was validated against the published age ranges for the Reclus R_1 and Mt. Burney MB_1 ash beds (Fig. 2), which were identified as cryptotephra deposits at Hooker's Point by Monteath *et al.* (2019). Calibrated dates and age ranges are reported at two sigma (95.4%) confidence throughout this study.

Plant macrofossil analysis

Sub-samples of peat measuring 4 cm^3 were prepared for macrofossil analysis by gently heating samples in 4% KOH solution for 10 minutes, before sieving through a 125 μm mesh with a standardised 5 L volume of water. The disaggregated macrofossil remains were examined at x40 to x150 magnification using a dissecting microscope. Identifications of *Sphagnum* branch leaves and monocotyledon epidermal tissues were made at x200 to x400 magnification using transmitted-light microscopy. Plant identifications were checked against the archive collection of fossil and modern type-samples held in the Palaeoecology Laboratory, University of Southampton. Identifications were also made with reference to Davies and McAdam (1989) and Woods (2000) for flowering plants native to the Falkland Islands, and Daniels and Eddy (1990) for *Sphagnum* mosses. Plant macrofossil abundance was assessed using the quadrat and leaf count method of Barber *et al.* (1994) for the main vegetative remains of the peat matrix, and a five-point scale of abundance (Walker and Walker, 1961), where 1 = rare, 2 = occasional, 3 = frequent, 4 = very frequent, 5 = abundant, for fruits, seeds and other small macrofossils. The macrofossil diagram (Fig. 3) was divided into six local plant macrofossil zones (LPMZs) using CONISS in TILIA software (Grimm, 1991).

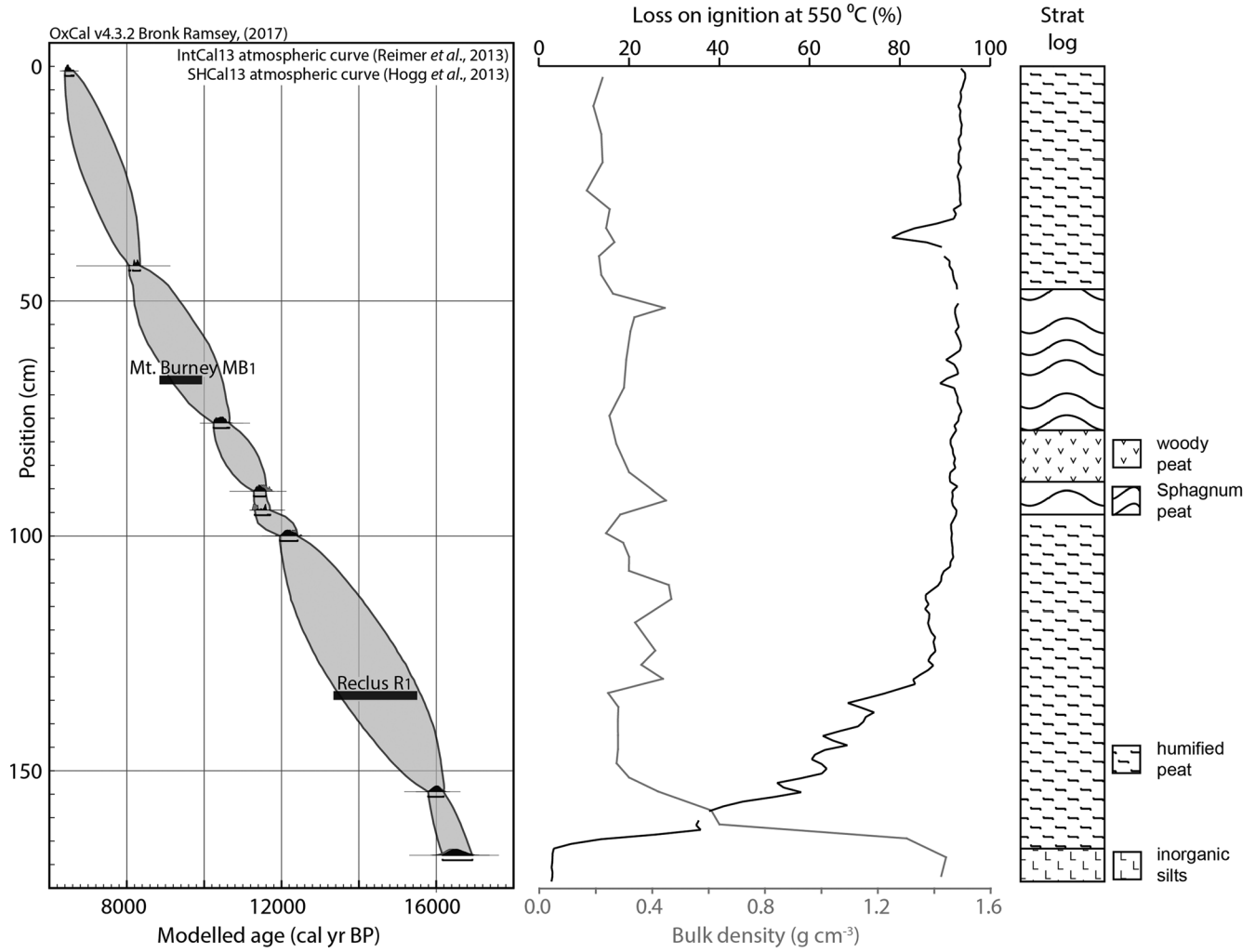

Figure 2. Oxcal age–depth model, loss on ignition values and bulk density data from the Hooker's Point sequence. The published age ranges for the Mt. Burney MB_1 (9950–8850 cal a BP; Stern, 2008) and Reclus R_1 (15 510–14 350 cal a BP; McCulloch *et al.,* 2005) tephra beds are shown as black bars. The position of these cryptotephra deposits in the Hooker's Point sequence are taken from Monteath *et al.* (2019). Bulk density measurements were made from measured 1 cm^3 peat samples.

Pollen analysis

Fifty-two pollen sub-samples taken at sampling intervals of 2 or 4 cm were prepared using standard techniques for the extraction of sub-fossil pollen and spores (Moore *et al.,* 1991). Initially, 10% KOH was used to deflocculate the samples which were sieved (150 µm) to remove coarse organic and inorganic debris. Clay and fine silt was removed using sieving at 10 µm. Hydrofluoric acid (40%vol.) was used to remove any remaining coarser, siliceous material. Samples were acetolysed for removal of plant cellulose and the concentrated pollen was stained using safranine and mounted in glycerol jelly on microscope slides. Pollen counts of 300 land pollen grains were made where possible and pollen frequencies were calculated as a percentage of total land pollen. The pollen diagram (Fig. 4) was divided into six local pollen assemblage zones (LPAZs) based on changes in the major taxa.

Diatom analysis

Samples from the basal 40 cm of the Hooker's Point sequence were examined by Prof. V. Jones (University College, London) for the presence of diatom frustules. The preparation of these samples followed standard protocols for siliceous microfossils (Battarbee *et al.,* 2001).

Table 1. Radiocarbon dates from the Hooker's Point sediment sequence with calibrated two sigma age ranges. Ages were calibrated using OxCal 4.2.3 (Bronk Ramsey, 2017), and the SHCal13 calibration curve (Hogg *et al.,* 2013).

Laboratory ID Code	Material	Position (cm)	Radiocarbon age ($^{14}C \pm 1$ SD yr BP)	13δC (‰)	Calibrated age range (cal a BP) (95.4%)
Beta-193400	Bulk (peat)	0–2	5700±40	−27.0	6628–6405
Beta-241334	Plant Macro	42–43	7390±40	−29.7	8341–8055
Beta-193401	Bulk (peat)	76	9250±80	−26.7	10650–10241
Beta-241335	Plant Macro	90–91	10030±40	−25.0	11749–11330
Beta-241336	Wood	94–95	9940±40	−27.0	11602–11242
Beta-193402	Bulk (peat)	100	10370±60	−27.3	12517–12000
Beta-241338	Plant Macro	154–155	13320±50	−27.1	16217–15822
Beta-193403	Bulk (peat)	168	13630±140	−27.7	16923–16055

Results and interpretation

Chronology

The chronology from the Hooker's Point sequence spans the Late-glacial–early Holocene (*c.*16 500–6450 cal a BP), including the interval of the Antarctic Cold Reversal (14 700–13 000 yr BP). The age–depth model shows close agreement with the published ages of the Mt. Burney MB_1 and Reclus R_1 tephra beds (Fig. 2), and suggests a near constant sedimentation rate throughout the analysed section. The date for earliest peat accumulation at Hooker's Point (*c.* 16 500 cal a BP) is close to that of 13 475 ± 50 BP (calibrated weighted mean:16 160 cal a BP) for the onset of peat growth at Lake Sulivan in West Falkland (Wilson *et al.,* 2002).

Plant macrofossil and pollen data

The results of the palaeoecological analyses from Hooker's Point are presented here and are divided into six vegetation zones based on changes in species abundance. Plant macrofossil data are described in Fig. 3 and Table 2, which are subdivided as LPMZs. The results of the pollen analysis are presented in Fig. 4 and Table 3 which are split into six LPAZs.

Synthesis of palaeoecological evidence from Hooker's Point

Changes in the pollen and plant macrofossil assemblages from the Hooker's Point peat sequence occur at similar points (allowing for slight sampling differences), and six principal phases of vegetation history are recognised between *c.* 16 500 cal a BP and *c.* 6450 cal a BP.

Phase one (pre-16 500 cal a BP) (174–168 cm)

The basal fine-grained (silt and sand) minerogenic sediments contain no pollen or plant macrofossils. The sediment is well sorted, lacks any coarser debris bands indicative of in-wash, and grades upwards sharply into a well humified peat at the boundary with phase two. The diatom assemblage from a sample taken at 172 cm includes aerophilous species (*Hanzschia amphioxys*, *Navicula mutica* and *Pinnularia borealis*), as well as species more characteristic of freshwater (*Brachysira* spp., *Navicula* spp. and *Diploneis* spp.) (Viv Jones, pers coms, 2011). We interpret the original depositional environment as a low-energy, freshwater, shallow-water body that formed under cold conditions at the time of the Last Glacial Maximum.

Phase two (16 500–15 940 cal a BP) (168–154 cm)

Phase two is characterised by the onset of organic accumulation and an amelioration of climate compared with phase one. The diatom assemblage (160 cm) is largely composed of aerophilous species (*Hanzschia amphioxys*, *Navicula mutica* and *Pinnularia borealis*) with additional freshwater taxa (*Amphora veneta*, *Pinnularia* spp., *Navicula* spp.) (Viv Jones, pers coms, 2011).The pollen in LPAZ-1 is dominated by Poaceae with lesser, but significant, numbers of Cyperaceae and Chenopodiaceae. There are woody lignified roots and leaves of *Empetrum* in the lower section of the peat, indicating on-site dwarf shrub development that is not represented in the pollen data, possibly because conditions were too harsh to allow flowering and pollination of these taxa. The low frequencies of Chenopodiaceae and occasional *Armeria*-type pollen grains suggest an arid, cold, steppe environment.

The onset of peat accumulation during phase two is likely to be associated with regional climatic warming beginning *c.* 17 500 cal a BP, coupled with a reduction in the west–east precipitation gradient as the Patagonian ice sheet retreated (McCulloch *et al.*, 2005; Pedro *et al.*, 2011). Organic accumulation, in response to these changes, must have occurred because of an increase in moisture availability and/or temperature. This may have only required a small climatic shift to step across a threshold to tip the accumulation/decay balance towards organic accumulation (Moore and Bellamy, 1974). The earliest phase of peat initiation in de-glaciated

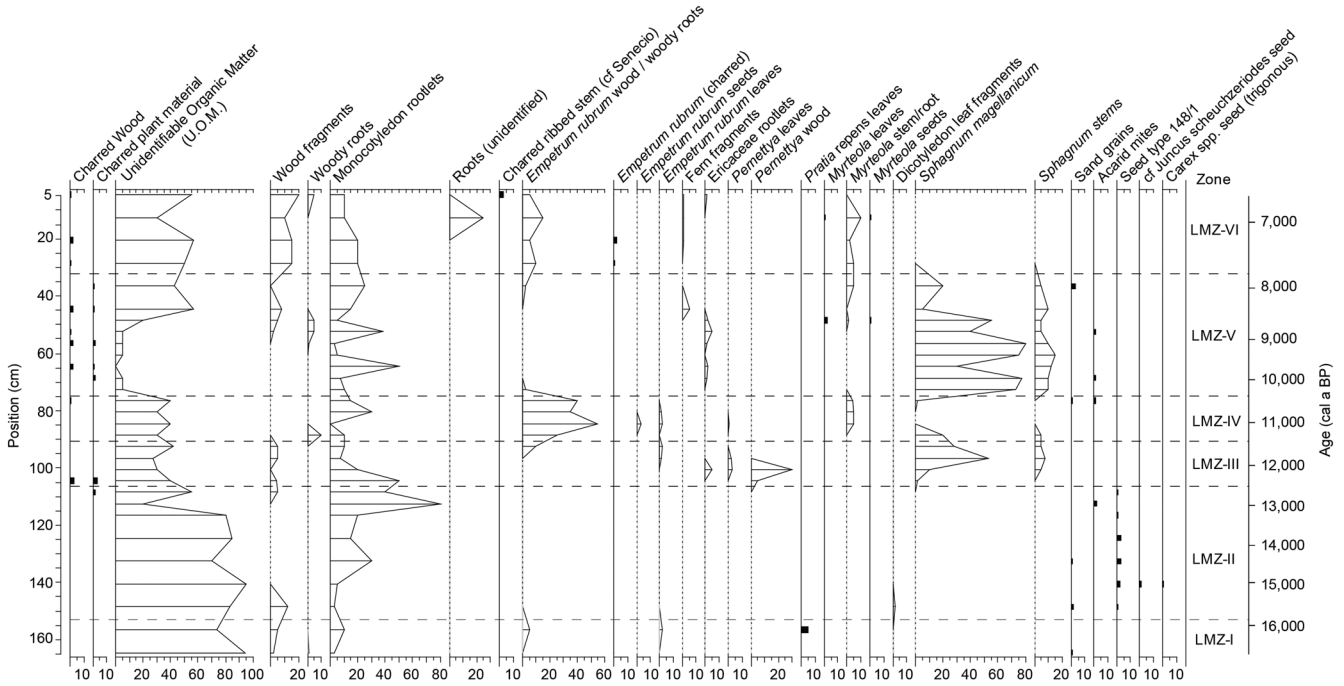

Figure 3. Plant macrofossil profile from the Hooker's Point sequence showing selected taxa. Small macrofossil remains are displayed as unlinked histograms on a scale from 1 (rare) to 5 (abundant). The main peat constituents are quantified as percentage cover of a grid graticule (Barber *et al.,* 1994) and appear as linked histograms.

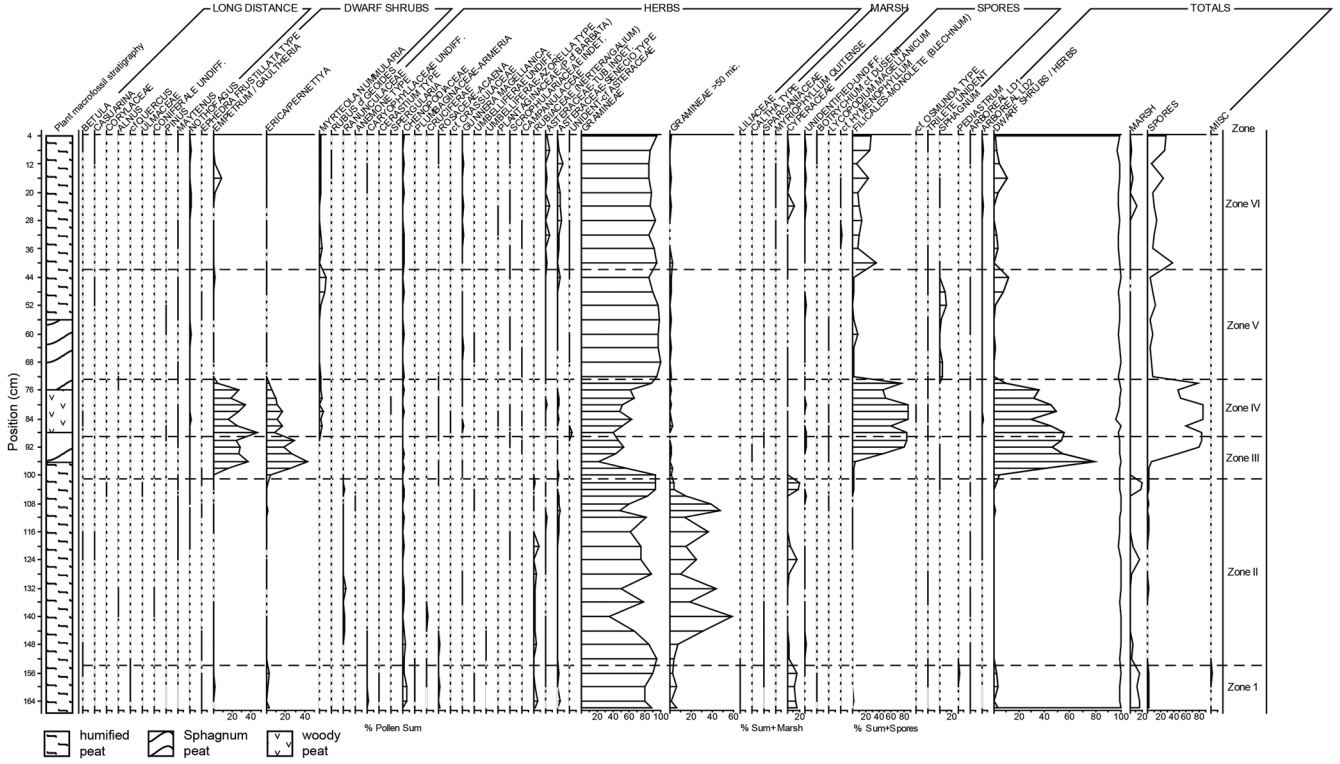

Figure 4. Pollen profile from the Hooker's Point sequence.

regions of Patagonia occurs *c.* 17 000 BP, and is associated with a rise in summer temperatures (Morris *et al.,* 2018).

Phase three (15 940–12 200 cal a BP) (154–101 cm)

Cyperaceae pollen frequencies decline, suggesting a drier local environment than phase two. The pollen assemblage (LPAZ-II) remains dominated by Poaceae and indicates a persistent cold climate, with a locally damp environment surrounded by open grass steppe. A lack of woody macrofossil remains suggests that it was not sufficiently dry to allow heath to become established on site. At *c.* 15 300 cal a BP, there is a sharp increase in the frequencies of a specific grass type of large (>50 μm) size (Poaceae 2) which persists in high values until *c.* 12 690 yr BP, after which they decline. Such large grains (outside of cereal varieties) come from a small number of genera/species (e.g. *Glyceria* and species of a halophytic tendency, including *Elymus*). From data by Barrow (1976), it appears that the Poaceae type 2 grains here are not from *Poa flabellata*, which has a size range of 27–33 μm on the polar axis. Groff (2018) has also noted that *P. flabellata* pollen is not distinguishable from the other grass taxa. However, Graff's measurements include *Elymus magellanicus* (Magellan wheatgrass) which has a size range to 37 μm on the polar axis. These

Table 2. Description of the plant macrofossil content of the Hooker's Point sequence.

Macrofossil zone (position in cm)	Description of the macrofossil content
LPMZ-VI 36–4 cm	Humification increases and the percentage of unidentified organic matter (UOM) remains high, peaking at 57%. Wood fragments dominate, many of which are *Empetrum rubrum*. Fern fragments, monocotyledon rootlets, charred plant remains and *Myrteola nummularia* stems/leaves are also present in the zone.
LPMZ-V 76–36 cm	*Sphagnum magellanicum* remains dominate the lower part of zone V but decline to 20% of the assemblage at 36–37 cm depth. Both monocotyledon rootlets and UOM are poorly represented in the lower part of the zone but increase in importance as the proportion of *Sphagnum* declines. Charcoal and charred leaf fragments occur in most samples. Other macrofossils include Acarid mites and the stems/roots of *Myrteola nummularia*. The top of the zone is marked by the disappearance of *S. magellanicum* which coincides with a sand deposition event.
LPMZ-IV 92–76 cm	*Sphagnum magellanicum* is replaced by the abundant remains of *Empetrum rubrum*, which include the wood, roots, leaves and seeds. The assemblage includes rare leaf fragments of *P. pumila* and the stems of *Myrteola nummularia*. UOM remains at 40% throughout the zone.
LPMZ-III 108–92 cm	This zone is defined by the arrival of *Sphagnum magellanicum* and *Pernettya pumila*. Good macrofossil preservation is shown by the survival of whole *P. pumila* and *Empetrum rubrum* leaves. *S. magellanicum* peaks at 33% of the macrofossil assemblage at the upper zone boundary.
LPMZ-II 156–108 cm	*Carex* and *Juncus* propagules are present together with an increased diversity of other herb taxa. Peat humification remains high. Monocotyledon rootlets increase in occurrence through the zone to a peak of 40% at the upper boundary. Evidence for sand deposition is also present at 132 cm and 148 cm depth. Charred plant material is present at the upper zone boundary at 108–109 cm depth.
LPMZ-I 164–156 cm	Fragments of *Pratia repens* leaf are present together with *Empetrum rubrum* leaves. Macrofossils are strongly humified and mainly composed of UOM and monocotyledon rootlets.

Table 3. Pollen zonation of the Hooker's Point profile.

Pollen zone (position in cm)	Palynological characteristics
LPAZ-VI 42–4 cm	Poaceae remain dominant (90–95%) with important Compositae types (Tubuliflorae indet. and *Senecio* type). *Gunnera magellanica* is consistent (1–2%). Cyperaceae increases in importance mid-zone (from 24 cm) with small numbers of *Myriophyllum cf. quitensis*. Spores of *Blechnum* type again become important with occasional *Hymenophyllum*. Long-distance pollen types recorded include *Nothofagus* and sporadic occurrences of *Meytenus*.
LAPZ-V 73–42 cm	Dwarf shrubs of zone IV reduce to absence. *Myrteola*, however, peaks at 38–40 cm (*c.* 8%). Poaceae attains its highest values (95%). Compositae types become important with Tubuliflorae indet. and *Senecio* type. *Blechnum* spores also diminish to low levels. *Sphagnum* is important in this zone with two separate peaks at *c.* 72 cm and *c.* 50 cm. Long-distance pollen types *Nothofagus* and *Meytenus* are present.
LPAZ-IV 89–73 cm	*Pernettya* declines progressively to low levels. *Empetrum* remains high but declines steeply at the top of the zone. *Myrteola nummularia* is incoming from the base of this zone and *Gunnera magellanica* becomes consistent. Poaceae type 2 (>50 μm) of the preceding zone declines to only occasional occurrences.
LPAZ-III 101–89 cm	Dwarf shrubs expand sharply with *Empetrum/Gaultheria* (45%) and *Pernettya* (45%) followed closely by *Blechnum* (to 90% sum+spores). Poaceae remain important but with reduced values (30%). *Nothofagus* is consistent in this zone at 1–2%. *Maytenus* is absent.
LPAZ-II 154–101 cm	Poaceae type 1 (<50 μm) (to 90%) is dominant with Poaceae type 2 (>50 μm; expanding to 45% declining to <10% at top of zone). There are two small peaks of Cyperaceae (to 20%) at 120 cm and 104 cm. Ranunculaceae are present only in this zone, Chenopodiaceae remain consistent but at reduced levels. Rubiaceae (to 5%) are absent at the top of the zone. The near-continental long-distance pollen types appear at 124 cm with *Maytenus* and *Nothofagus*.
LPAZ-I 168–154 cm	Poaceae are dominant (to 90%) with Cyperaceae (19%). Chenopodiaceae (*cf. Colobanthus*), *Erica/Pernettya* (1–2%), *Ephedra frustillata* and Rubiaceae (4%) represent. Algal *Pediastrum* are present.

grains were mounted in silicone oil, whereas here, glycerol was used and would account for the greater size. Thus, we tentatively attribute Poaceae type 2 to this species. This accords with the coastal distribution of this grass. We do not attribute any palaeoclimate significance to the change in Poaceae frequencies during this interval; however, a more detailed resolution of this taxon is being sought. Long-distance pollen types *Nothofagus* and *Maytenus* first appear in the Hooker's Point sequence during this period (*c.* 13 260 cal a BP).

Phase four (12 200–10 250 cal a BP) (101–73 cm)

The start of phase four saw the onset of a change towards wetter local conditions at Hooker's Point. However, these soon become drier as *Sphagnum. magellanicum* was replaced by *Empetrum rubrum c.* 11 330 cal a BP. Most importantly was the progressive establishment and maturation of a dwarf shrub and fern community. Macrofossil remains of dwarf shrub and ericaceous plants are common and the peat contains larger numbers of fungal hyphae. Initially, *Pernettya* started to expand followed closely by *Empetrum/Gaultheria.* The former is likely to be the evergreen shrub *Pernettya pumila* since abundant (30%) macrofossils of this species occur at this level (Fig. 3). Subsequently, ferns (*Blechnum* spp.) became dominant. This habitat change is also reflected by a substantial reduction in Poaceae and a decline to almost absence of Poaceae type 2. The former may, however, be a within (pollen) sum percentage reduction caused by the expansion of dwarf shrubs. *Sphagnum* spores occur in low frequencies in the pollen record and there are abundant macrofossil remains of *S. magellanicum* throughout this zone. This phase also saw the appearance of *Myrteola nummularia* (teaberry) which is recorded consistently throughout the upper part of the section and in today's vegetation assemblage at the sample site. Its appearance at the start of the Holocene may reflect a change in climate at this time.

Phase five (10 250–8210 cal a BP) (73–42 cm)

This phase records the second shift to wetter conditions recorded at Hooker's Point. The dry ericaceous and fern community was replaced, at least locally, by the development of *Sphagnum* peat. Despite this change, there is clear evidence (charred macrofossils) for repeated burning on the site. *Empetrum rubrum* is resinous and will burn even when damp and, although some of the burning is linked to periods of *Empetrum* heath development, there is also evidence for burning during the *S. magellanicum* bog phase. Similar burning episodes are known from early Holocene peat bogs on West Falkland (Barrow 1978) and in southern South America (Heusser, 1989; Whitlock *et al.,* 2007; Moreno *et al.*, 2018), where they have been attributed to increased aridity and changes in the position of the Southern Westerly Wind Belt. The initial wet shift is followed by a trend towards drier conditions as *Sphagnum* macrofossil frequencies decline and ericaceous communities (notably *Myrteola*) become re-established on site.

Phase six (8210–6450 cal a BP) (42–0 cm)

This period saw the establishment of drier conditions at Hooker's Point, indicated by a decrease in the abundance of *Sphagnum* remains, an increase in unidentified organic matter and Filicales macro-remains, as well as Poaceae and *Myrteola* pollen frequencies.

Discussion

Late-glacial–early Holocene environmental change in the Falkland Islands

The Hooker's Point record demonstrates the persistence of a treeless environment throughout the Late-glacial–early Holocene. Together with Holocene pollen studies (Barrow, 1976, 1978; Turney *et al.*, 2016; Thomas *et al.*, 2018), this record shows that the Falkland Islands have not supported any higher arboreal or large shrub vegetation for at least the last *c.* 16 500 years. While vegetation communities within this environment do appear sensitive to climatic change, the changes in floral composition are subtle relative to those that took place in the northern hemisphere during the time period spanned by the Hooker's Point sequence. It is likely that a combination of continued high wind speeds and shallow soil depths prevented

the establishment of trees in the archipelago, regardless of changes in temperature or precipitation.

The origins of peat accumulation in the Falkland Islands

Peatlands in the Falkland Islands, including Hooker's Point, developed at the edge of the climatic envelope for global peat initiation because of the low annual precipitation (Morris *et al.*, 2018). Despite this, peatlands are extensive across the archipelago, and in some coastal locations (e.g. Beauchêne Island) may form 'extraordinary' sequences exceeding 11 m in depth, characterised by extremely high carbon density (Smith and Clymo, 1984; Evans *et al.*, 2019). We hypothesise that peat accumulation in the Falkland Islands is promoted by the recalcitrant litter quality of the native grass communities, evident in the Hooker's Point macrofossil assemblage (Fig. 3). Species within these communities, such as *Cortaderia pilosa* (whitegrass) and *Poa alopecurus* (bluegrass), are adapted to low nutrient soils and high wind speeds, so produce leaves with thick, fibrous, epidermal layers that are highly resistant to decay (Davies *et al.*, 1990). While whitegrass is dominant in the contemporary setting, bluegrass was far more extensive prior to human disturbance, and was described as 'so harsh and rigid as to be quite unpalatable to cattle' by Hooker (1847). The durable litter produced by these grasses provides a means to tip a catchment balance towards organic accumulation in what would otherwise be a marginal environment for peatland development. Studies of Holocene raised peat accumulation (just after the fen-bog transition) in Europe have also shown that similar litter accumulation processes operated in the northern hemisphere, where peat accumulation following the fen-bog transition often occurred in dry climatic phases during the early to mid-Holocene. In these cases *Eriophorum vaginatum* builds a 'foundation' stratum of highly humified peat. This deposition seems to have been instrumental in providing suitable semi-permeable strata for later development of the domed water tables of Atlantic raised bogs under more humid climatic conditions. (Hughes *et al.*, 2000; Hughes and Barber, 2004).

Due to the comparatively dry climate, peatlands in the Falkland Islands are assumed to be relic systems that formed in the past under wetter conditions (Otley *et al.*, 2008). However, Hooker's Point continued to accumulate organic material at a near linear rate throughout millennial-scale climate perturbations during the Late-glacial, when climate is likely to have been at least as dry as present conditions (Fig. 2). This suggests that peatlands in the Falkland Islands may be continuing to accumulate organic matter, and importantly carbon, under the present climate. Payne *et al.* (2019) report highly variable carbon accumulation rates in Falkland Island peatlands, which suggests that peat systems in the archipelago are affected by a range of drivers; for example, climate change, mineral input, guano input and burning. The study of peatland palaeoecology in drier, marginal, environments such as the Falkland Islands has implications for modelled projections of peatland persistence under different future climate change scenarios (e.g. Ise *et al.*, 2008; Gallego-Sala and Prentice, 2013). In these modelling experiments, continued peat accumulation is often assumed to be dependent on a permanently high water table. However, pollen and plant macrofossil evidence from the Hooker's Point sequence suggests that peat accumulation can continue in comparatively dry environments, where peatland water tables may be low, if the local vegetation is decay-resistant.

Falkland Islands vegetation – climate sensitivity

The Hooker's Point pollen and plant macrofossil records are insensitive to regional cooling during the ACR (14 700–13 000 yr BP), which is widely expressed across the southern hemisphere, and which would have affected the Falkland Islands (Pedro *et al.*, 2016). Glacier, oceanic and terrestrial records in southern South America record the declining temperatures during the ACR, and modelling simulations suggest that the Falkland Islands would have experienced a (0.5 °C) cooling and local drying (Pedro *et al.*, 2016). The apparent climatic insensitivity of the Hooker's Point palaeoecological record during this period suggests that conditions in the Falkland Islands prior to the ACR cooling were already too harsh for the establishment of thermophilous plant species. Instead, cold and wind-adapted grass taxa (e.g. *Cortaderia pilosa* in the contemporary setting) persisted almost throughout the Late-glacial period despite millennial-scale perturbations in climate, which are expressed in regional records (Pedro *et al.*, 2011; Kilian and Lamy, 2013). Conversely, the palaeoecological record from Hooker's Point demonstrates a dynamic vegetation assemblage between 12 200–8 000 cal a BP (Fig. 5), characterised by sharp shifts between wetter (*Sphagnum magellanicum*) and drier (*Erica*) indicators. Turnover between these species occurs during the latter half of the Younger Dryas time period (12 900–11 700 cal a BP) and the Southern Hemisphere Early Holocene Thermal Maximum (11 500–8500 yr BP). These time periods are associated with warming temperatures (Kilian and Lamy, 2013) and shifts in the latitudinal position and/or strength of the Southern Westerly Wind Belt (Vanneste *et al.*, 2015; Moreno *et al.*, 2018), which would have influenced precipitation in the Falkland Islands. These findings show that the flora of the Falkland Islands was sensitive to past climate change, in contrast to previous studies which suggested a stable, unresponsive, vegetation assemblage during the Late-glacial and Holocene (Barrow, 1976, 1978; Clarke *et al.*, 1998). Despite these changes, no new species became established at Hooker's Point during this period (with the exception of *Myrteola nummularia*), suggesting that invasive species remained unable to colonise the local environment despite the increasing temperature and moisture availability, indicated by increases in Ericaceae species and *Sphagnum magellanicum*. It is likely that the exclusion of invasive species is due to a combination of the high wind speeds affecting the archipelago, and its isolation, which limit the establishment of non-wind-adapted flora in the contemporary setting, and may continue to do so even under future climate warming.

Long-distance pollen and the Southern Westerly Wind Belt

The near-continental long-distance pollen component identified at Hooker's Point comprises *Nothofagus* (*N. antarctica, N. pumilla*) and *Maytenus*, which are sourced from southern Chile and Argentina. Similar findings are reported from Holocene records in the Falkland Islands and South Georgia (Barrow, 1978; Strother *et al.*, 2015; Turney *et al.*, 2016; Thomas *et al.*, 2018). Clark *et al.* (1998) also noted a low influx of arboreal pollen (<1%) (mainly of *Nothofagus*) in the Late Pleistocene (*c.* 26 000–36 000 cal a BP) sediments from East Falkland. Changes in the abundance of *Nothofagus* pollen delivered to eastern Patagonia and the Falkland Islands during the Holocene have been interpreted as wind-dependent (Mayr *et al.*, 2007; Turney *et al.*, 2016; Thomas *et al.*, 2018), and it is therefore likely that the first appearance of *Nothofagus* pollen in the Hooker's Point sequence is linked with a change in the

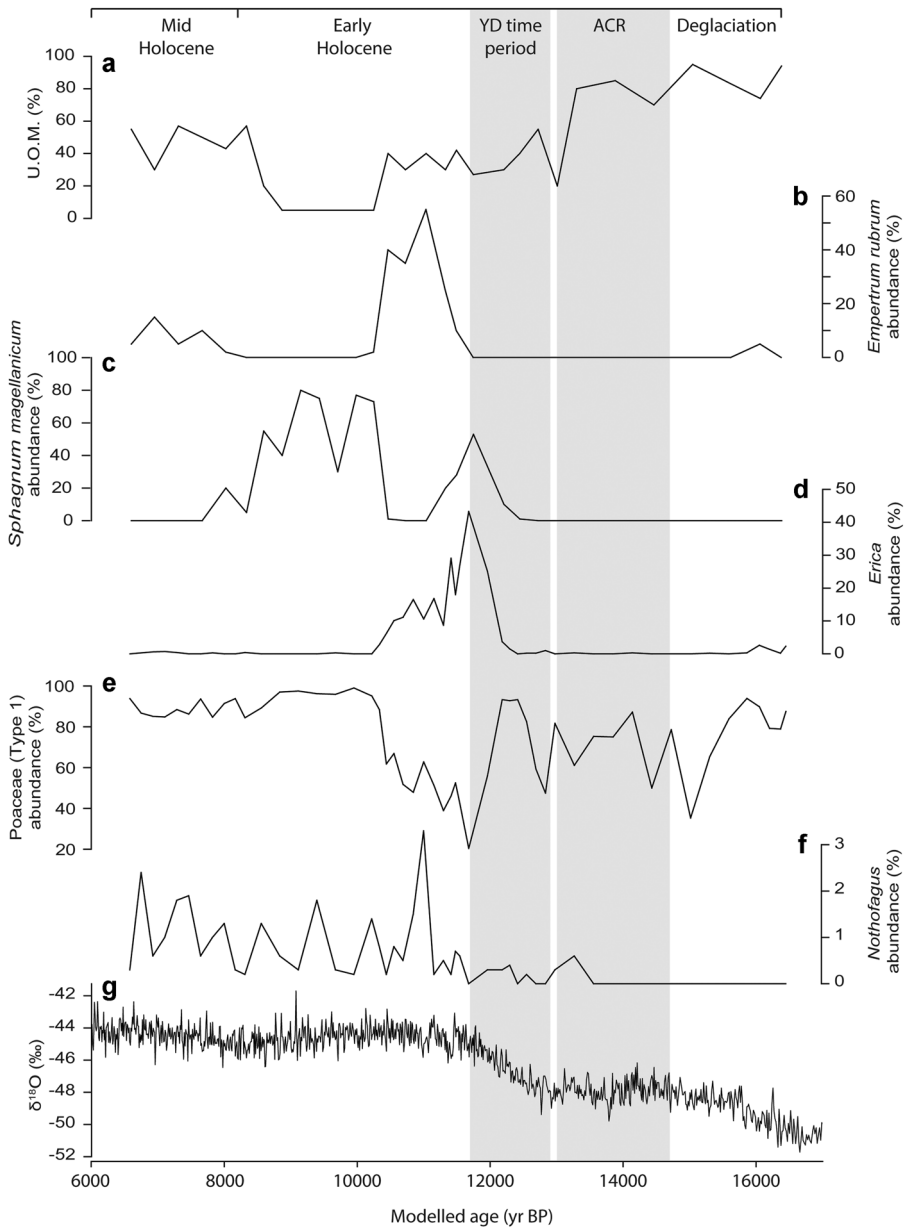

Figure 5. (a–f) Key pollen and plant macrofossil taxa from Hooker's Point plotted against age. (g) The EPICA Dome C $\delta^{18}O$ record (EPICA community members, 2006). YD=Younger Dryas, ACR=Antarctic Cold Reversal; UOM=unidentified organic matter.

strength and/or position of the Southern Westerly Wind Belt. The appearance of *Nothofagus* in Hooker's Point *c.* 13 330 cal a BP (Fig. 5) occurred late in the ACR and coincides with a shift in carbonate isotope values in Laguna Potrok Aike (13 400–11 300 cal a BP; Mayr *et al.,* 2013), and the expansion of *Nothofagus* near Lago Lynch (*c.* 13 300 cal a BP) (Tierra del Fuego) – also linked with a change in the Southern Westerly Wind Belt (Mansilla *et al.,* 2018).

A second 'extra-long-distance' pollen component is present at Hooker's Point which includes *Betula, Casuarina, Alnus,* Coryloid, *cf. Quercus,* Ulmaceae and *Pinus. Quercus* and *Betula* are the earliest extra-long-distance arboreal pollen arrivals with their first occurrences at *c.* 16 200 cal a BP and *c.* 15 860 cal a BP, respectively. Barrow (1978, 1983) also noted *Alnus* in sediment profiles from South Georgia which he suggested may have been a contaminant. However, similar rare occurrences are evident in pollen profiles from both sub-Antarctic islands (Hafsten, 1951; Cranwell, 1969; van der Knaap and van Leeuwen, 1993) and the Antarctic continent (Hafsten, 1951, 1960a, 1960b; Linskens *et al.,* (1991); Linskens *et al.,* 1993). These repeated records of extra-long-distance taxa may represent either: i) ultra-distal atmospheric pollen transport, or ii) contamination. Given the now frequent records, an extra-long-distance, northern hemispheric source for this pollen is plausible. However, replicated results from samples analysed in southern hemisphere control laboratories are needed to test both hypotheses.

Conclusions

The Hooker's Point sequence, in conjunction with Holocene pollen records (Barrow, 1976, 1978; Turney *et al.*, 2016; and Thomas *et al.*, 2018), show that the Falkland Islands have remained treeless for a least the last *c.* 16 500 years. The landscape of the Falkland Islands is, therefore, an unusual example of a maritime environment that has developed without trees and higher shrubs. This rare environmental history provides an interesting ecological control site that may be used for the study of fluvial development under temperate, treeless, conditions.

Peatlands in the Falkland Islands have previously been considered to be relic systems that formed during wetter conditions in the past (Otley *et al.*, 2008). However, continued organic accumulation at Hooker's Point throughout the Late-glacial demonstrates that Falkland Island peatlands have developed under dry conditions in the past, and may continue to do so today. This finding suggests that some peatlands in

marginal environments can remain valuable carbon sinks even under low precipitation regimes.

The vegetation of Hooker's Point appears insensitive to the regional cooling during the ACR, but shifted toward a dwarf shrub-dominated community during the latter half of the Younger Dryas time period and Southern Hemisphere Early Holocene Thermal Maximum. The decline of tussac grass dominance under warming has implications for future vegetation communities in the Falkland Islands which are expected to be subjected to a warmer climate.

The first appearance of long-distance *Nothofagus* pollen in the Hooker's Point sequence *c.* 13 330 cal a BP is likely to be wind-dependant, and occurs late in the ACR. This time period is associated with changes in the strength and/or position of the Southern Westerly Wind Belt, and shifts in wind proxies in Laguna Potrok Aike (Mayr *et al.,* 2013) and Tierra del Fuego (Mansilla *et al.,* 2018) closely overlap the *Nothofagus* pollen record from Hooker's Point.

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Abbreviations. ACR, Antarctic Cold Reversal; LPMZs, local plant macrofossil zones; LPAZs, local pollen assemblage zones; UOM, unidentified organic matter.

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